CONSTRICTION OF TWIGS BY THE BAG WORM AND INCIDENT EVIDENCE OF GROWTH PRESSURE.*

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INTRODUCTION.

For a number of years many branches of arbor vitae (*Thuja occidentalis*) in the Missouri Botanical Garden showed signs of disease and gradual dying from the tips of the branches inward. A careful examination of the twigs showed a condition represented on plate 20, figs. 1, 2 and 3. At a short distance from the end of the twig a swelling was usually found, which in the case of twigs which were still comparatively green was very small, but in many cases reached a size of four and five times the diameter of the twig below the swelling. The part of the branch above the swelling was usually very much larger in diameter than the branch below the swelling. Where the swelling was at all large the parts of the branch towards the outside of the tree were usually found either in a dead or dying condition. In every case the diseased branches showed marked tendencies towards the formation of secondary buds and branches, so that frequently the tip of a branch had the appearance of a small broom (pl. 20, fig. 3). After looking at a number of trees the swelling was finally found to be due to the girdling action of the bands of the common bag worm (*Thyridopteryx ephemeraeformis* Haworth), (pl. 20, fig. 2). A great many instances of the swellings with the bag worm still in position were found in the vicinity of St. Louis and in other parts of the country; and in all of the older swellings where no bag was visible, the band of the worm was found still encircling the branch.

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There seems to be no doubt therefore that the band of the bag worm was responsible for the swellings, serving as a kind of ligature which prevented the passage of elaborated materials from the outer part of the branch towards the trunk, and acting just as a wire would when wound around a growing twig. In the course of time the part of the branch above the band increased in size until such time as the passage of the elaborated material was prevented entirely, resulting in the final death of the branch.

After attention had been called to the occurrence of the bags on arbor vitae and the girdling effect which they exerted, a search of the various trees in the Garden and in the country around St. Louis showed that this action of the bag worm on arbor vitae was an extremely common one; in fact it was almost impossible to find a tree of arbor vitae which did not show one or more of the swellings.

LIFE HISTORY OF THE BAG WORM.

In order to understand the manner in which the insect kills the branch it will be necessary to refer briefly to its life history. The common bag worm (*Thyridopteryx ephemeraeformis* Haworth*) hatches from eggs which have remained on the trees in the bags over winter. In the vicinity of St. Louis the larvae appear on shade trees in the early spring just as the buds are opening. The larvae feed on the young leaves, and very shortly after their appearance begin to spin small bags which they carry about with them. As the insect grows older practically nothing of the larva is visible except the anterior portion of its body, the rest of its body being encased in the bag. Towards the latter part of the summer, from the beginning of August on, the larvae attach the bag to some twig near the outer part of the tree; they do this by spinning a band

* For a good description of this insect and its habits, see Felt, E. P. Insects injurious to elm trees. (5th Annual Report, Fisheries, Game & Forest Commission of New York, p. 359, 1903).

around the branch in such manner that when the bag is finally fastened it is suspended from the branch, as shown in plate 21. The band varies in width and in thickness. It is closely adapted to any irregularity in the bark of the particular twig, and is so wound around the twig that it can be moved laterally only with difficulty. It is in no way pasted or glued to the bark, as can easily be shown by cutting the band at any point, which will cause the cocoon to drop. The insect will attach its bands, almost without fail, only on one-year-old twigs. Whether this is due to the fact that it is upon these twigs that it has been feeding, or whether it is due to the fact that these twigs are usually smallest, I have not been able to determine. That the size of the twig has something to do with the weaving of the band is shown by the following experiment: In order to test the strength of these bands, the writer desired to get bands of as great a length as possible. A number of the larvae which were found ready to attach themselves to twigs were taken and placed on twigs having a diameter of about three-eighths of an inch; in no case did these transplanted larvae weave a band around a twig of this size. When they found that they could not get away from the large twig they made a band which they glued to the lower side of the twig, thereby suspending the cocoon; when the branch was one-fourth inch thick or less they invariably made a band completely around the twig. The relation between the size of the twig and the number of bands is shown in detail in Table I. After the band has been woven, the cocoon hangs on the tree over winter and into the next spring, in fact until about the end of June of the following year. Some six weeks or more after the leaves have fully opened one can pass under trees which have been covered with the bag worms during the winter and find hundreds of them lying on the ground under the trees. The falling of the bags is brought about by the bursting of the bands by the twigs as they increase in diameter. That

this is the cause of the bursting of the bands was determined repeatedly by noting that in no case would the bands burst until a considerable formation of wood took place in the twig to which the bags were attached. The bursting of the bands took place at almost any point in their circumference except at the point where the bag was attached to the band; in other words, the weakest point in the bands usually was at some point away from the bag itself. This was a fact of considerable interest, the force of which will be referred to again further on.

FORMATION OF THE SWELLINGS.

By the end of July practically all of the bands of the previous year have dropped from the trees; here and there however, one finds a bag which has not fallen. Upon examination it will be found that the band of this particular bag still passes intact around its twig; and should this bag remain upon the twig until September, one will find that a swelling, such as the ones referred to above, has begun to form. It would appear from this that any particular band which remains throughout the summer has been strong enough to resist the forces exerted by the growing twig as it expanded in the formation of new wood, and that the band then acted as a ligature. All of the conditions for the formation of the swelling were thereby brought about.

As the bag worm occurs on other trees besides the arbor vitae, an examination was made of trees in the Garden and in the streets of St. Louis for the purpose of finding out whether the girdling action noted for the arbor vitae trees also took place on other trees. After a few days of searching it was found that practically every tree species upon which the bag worm occurred was girdled now and then very much as were the arbor vitae trees. On some species the girdling action appeared to be very common, particularly on the sycamore and soft maple, but nowhere did it occur as frequently as with the arbor vitae. Thus

far the constrictions have been found on the following trees: soft maple, sycamore, willow, poplar, sassafras, red gum, white oak, locust, apple, cherry, hemlock, bald cypress, Virginia pine, Deodar cedar, larch, *Juniperus virginiana*, *Juniperus occidentalis*, *Thuja occidentalis*, and *Juniperus chinensis*. It is very probable that similar swellings will be found on other species of trees where the bag worm occurs.

The effect of the girdling action of the band differed very materially on different kinds of trees. Two types may be distinguished. In one case the band evidently has stopped the passage of plastic materials through the bark absolutely. As a result of this an accumulation of these substances has taken place on the outer side of the band and the cambium layer at this point has formed wood cells and bark cells to an enormous degree, as a result of which the outer part of the twig has grown very much in diameter, particularly so immediately beyond the band. The portion of the twig towards the tree has practically stopped growing entirely; cases of this kind are shown on pl. 20 and pl. 24.

In the second case the pressure exerted by the band was evidently not sufficient to entirely stop the passage of plastic materials, or only temporarily so. In this case, a slight swelling of the portion of the branch outside of the band will be formed after a month or so, following the beginning of wood development. At the end of the first year a condition such as is shown on pl. 22, fig. 1 is found. This represents a two-year-old maple twig. It will be noted that the outer part of the twig is somewhat larger than the part towards the trunk, but that there is also a considerable increase in diameter of the twig on the side of the band towards the trunk; this is shown likewise for the willow, oak, red gum, sycamore, etc. (pl. 23). After another year's growth a still further increase in the diameter of the outer part of the twig has taken place (pl. 22, fig. 3), but the inner portion of the twig, towards the trunk, has like-

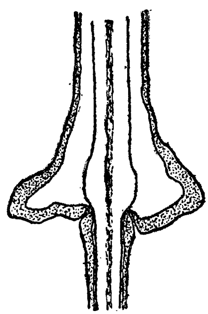
wise increased in diameter. Two distinct flat surfaces are thus formed where the swellings above and below the band face one another. In the course of time, in certain cases, two years after the band has been on the twig, these two surfaces unite completely around the twig (pl. 22, fig. 2), and there is to all intents and purposes a union between the two swellings which resembles in many respects the union which takes place between two pieces of callous tissue after they meet from opposite sides of a wound. After the two surfaces have united, the development of the branch goes on as if there had been no girdling; and the band of the bag worm is enclosed within the swelling and may remain there for an indefinite period. Plate 22, fig. 4 shows a branch of a maple tree ten years old. There are no signs visible on the outside, of any disturbance due to the insect except the old cocoon, which is still hanging from the lower side of the branch, with not only the slender filament, but also a large portion of the upper part of the cocoon enveloped by the wood of the maple. In the case of the sycamore, maple and other rapidly growing trees the disturbance caused by the bag worm is generally only a temporary one, and in the many hundred cases found on these trees, there is not one instance where death followed the failure of a twig to break the band.

The formation of the single swelling on the outside of the band is confined singularly enough almost wholly to the coniferous trees, in some of which it is extremely striking. The most remarkable cases of excessive swelling with subsequent death were found on a young tree of the Deodar cedar on the grounds of Tulane University, in New Orleans (pl. 24, fig. 5, 7, 8). A similar large swelling was found on a tree of *Pinus virginiana* growing near Washington, D. C. (pl. 24, fig. 1). The only case of this kind among dicotyledonous trees was found in the locust (*Robinia pseudacacia*). Four trees of this species were found in a park in New York City with some ten swellings;

of these one is shown on plate 23, fig. 2. In every case the outer part of the branch was dead, and no growth had taken place in the twig between the constriction and the tree. The marked inability of the conifers to adapt themselves to these unusual circumstances is very striking.

STRUCTURAL CHANGES CAUSED BY THE BANDS.

The changes which take place in the branch of a tree as a result of the pressure exerted by the bands of the bag worm are of two distinct types, one of which may be illustrated by the arbor vitae and the other by the maple or sycamore. In the arbor vitae and other conifers, growth starts under the band in June following the year in which the band is attached to the tree. Where the expanding force of the tree is great enough to burst the band, or where the band is weak, no change takes place which differs in any way from the normal development of the particular twig. Where the band happens to be a strong one which cannot be burst by the growing twig, changes of a very radical nature make their appearance a month or more after the beginning of the growth period of the twig. A longitudinal section made through such a twig after a year's growth of the arbor vitae is shown in fig. 1. It will be noted that the cambium layer formed a number of rows of wood cells immediately under the band, but that after a very brief period the formation of wood in the twig, beginning at the band and below it, stopped entirely, while the part towards the outside of the band continued to grow vigorously, producing the peculiar swelling above referred to. The most striking change in the immediate vicinity of the band consists in the enormous development of bark. Immediately above and below the constriction the bark is two or three times as thick as it is normally (fig. 1). The wood cells formed immediately

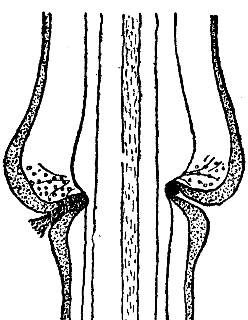


1. ARBOR VITAE.

beyond the constriction continue to grow normally. The new wood formed above the band differs but little from the normal type; the tracheids are somewhat shorter than the normal ones, but the chief difference lies in their manner of arrangement, for a complete turning takes place in their position. Instead of growing longitudinally they grow at right angles to the long axis of the twig. In other words, in the region of the swelling all wood fibers formed during the first year under the constriction extend around the twig instead of longitudinally. In the arbor vitae the normal direction of the wood fiber is rarely re-established except in such twigs as are growing vigorously, because before a resumption of normal growth is possible the twigs usually die. Where the development of the swelling is very large, a decided buckling of the cells of the bark frequently takes place.

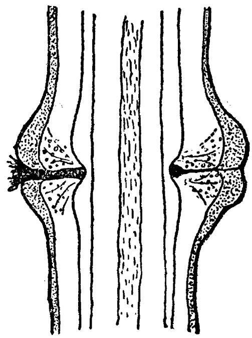
An examination made of a two-year-old constriction in the latter part of the summer, shows the presence of very large amounts of starch in the bark, medullary rays and pith ring in the part above the constriction, while there is practically none in the part below it. An inch or more below the constriction no starch whatever occurs.

The changes which take place in hardwoods differ very materially from those just described for the arbor vitae. In the spring or early summer following the constriction, both the wood and bark continue to form under the band, both above and below it. Figure 2 represents an early stage in a maple constriction. After a month or more the wood cells appear as if constricted immediately under the band. A diversion of the wood cells from their normal longitudinal direction to one at right angles takes place in the sycamore, maple and other hard woods very much as it



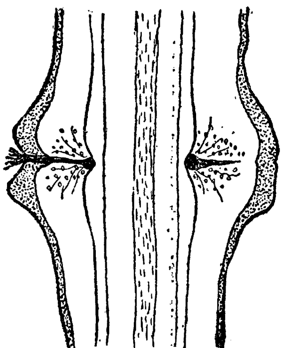
2. SOFT MAPLE.

does in the arbor vitæ, but it occurs on both sides of the band. As a result of the growth both above and below the band, two lips or rings of tissue are formed (fig.2–4). which at first are separated, but which soon meet above the band and become closely appressed (fig 3). At the end of the first year the two lips have usually joined, and a continuous ring of wood fiber has once more been formed. As soon as the union has taken place between the two lips the wood fibers once more assume their normal longitudinal position (fig. 4).



3. SOFT MAPLE.

The parts immediately above and below the band show an abundant supply of starch throughout the summer and late into the fall, from which it is evident that the flow of nutrient substances from the outer part of the twig to the lower part is never entirely stopped by the constriction.



4. SOFT MAPLE.

The wood cells formed under the band during the process of healing differ considerably from the normal wood tissue. The first wood cells formed under the band in June, following the year when the band is first attached to the twig, are normal in every respect. Although the band is fastened firmly around the twig, it is probable that it at first exerts very little pressure upon the growing cambium cells; it is probable likewise, that the band stretches to some extent during the first month or two following the beginning of the growth period of the twig. At a certain point, however, a time is reached where the band no longer stretches,

and from then on the band exerts an increasing amount of pressure upon the underlying cambium cells. A word should be said at this point as to the structure of the band. It is composed of a series of fine strands of silk which are densely interwoven, forming a very compact mass; the individual fibers appear to be pasted together with a cementing material; they are closely adapted to the irregularities of the bark, so that the pressure which the band as a whole exerts is a very even and regular one.

After the pressure has begun to act a marked change in the character of the wood cells formed under the band is noticeable, which gradually becomes more marked as the amount of wood formed below the band increases. After about six weeks all further formation of wood tissue under the band ceases. On plate 25 are shown sections of normal maple wood (fig. 1) and of a portion of the wood formed under a band in a maple twig (fig. 2); likewise sections of wood of the red gum from normal (fig. 3) and constricted regions (fig. 4); and plate 26, figs. 1 and 2, shows two photomicrographs of a cross section of maple and red gum twigs immediately under the band. It will be noted that as the pressure increases the number of vessels decreases proportionately, and at a period when the growth has almost ceased, the formation of vessels has almost stopped. Under the increased pressure the wood cells take on an entirely different appearance; instead of the comparatively thin-walled, large-lumened tracheids, one finds thick-walled, very small-lumened tracheids forming, which continue to be formed up to the very time when all growth ceases. The vessels which form at the period of greatest pressure show a tendency to become round and thick-walled, as well as smaller in diameter. The medullary rays show a decided tendency to buckling. Instead of growing out in a straight line radially, they bend towards one side or the other as if pulled laterally. This bending is more striking in some instances than others. It is of

further interest to note that the very last wood cells formed before all growth ceases still have all the characteristics of wood fiber; they are smaller, to be sure, but there is no mistaking them for anything but typical wood cells. Immediately between the last wood cells formed and the band, will be found the very much compressed and shriveled remnants of the original bark, which in the majority of cases has been so thoroughly compressed that it appears as a dark, opaque line, in which no structure can be discerned.

The influence which pressure has upon the development of wood tissue was first investigated by Sachs (8) and DeVries (9). Sachs, in an attempt to explain the cause of the formation of spring and fall wood in trees, assumed that the cambium is acted upon by a definite pressure exerted by the bark, and that this pressure increases from the spring to the fall, equalizing itself during the winter; he took the formation of cracks in the bark in the spring as an evidence of the growth energy of the woody cylinder overcoming the bark pressure acting against it. DeVries, in an endeavor to explain the causes of spring and fall wood, made a series of slits in the bark in the fall, as a result of which he noted the formation of spring wood. This he explains by imagining that the bark pressure was destroyed because of his making slits, and consequently large-lumened cells were formed. He likewise placed a number of ligatures on branches in the spring and observed the formation of summer wood under these ligatures. He concludes from these experiments that the radial diameter of the wood elements is determined by the bark pressure exerted during their formation; and furthermore that the number and size of the vessels in any one wood ring are determined by the bark pressure which happens to be experienced at the time of formation of this particular ring, higher pressures resulting in fewer vessels which are of smaller diameter.

Krabbe (5) disagrees with both Sachs and DeVries as to the existence of bark pressure. In a series of extensive experiments he shows that the difference in the bark pressure during the spring and summer is so small that it could not possibly account for the difference in structure of spring and summer wood. In another series of experiments Krabbe (6) increased the bark pressure by means of wooden cylinders formed into a chain, to which weights were attached; by increasing the pressure on the growing tree he found that one can increase the bark pressure two or three times without influencing the growth in thickness of the branch. For conifers he found that a pressure of from three to five atmospheres slowed up the growth and changed the radial diameter of the cells, while a pressure of ten atmospheres stopped the growth entirely. For broad-leaved trees he found that a pressure of from five to seven atmospheres reduces growth; but he failed to determine the upper limit of growth. In discussing the morphological changes which the wood cells undergo as the pressure increases, he notes in particular a reduction in the number of cells formed as the pressure increases, and the gradual change of the vessels from an elliptical cross-section to circular. Another point which he notes is that the cambial cells continued to form wood cells of a normal character, irrespective of any pressure which he was able to bring to bear upon them. The newly formed wood cells, which under ordinary circumstances are capable of expanding until they reach a size very much larger than when first formed, are materially influenced by the pressure, and as the pressure increases, the stretching of the newly formed wood cells may cease altogether, thereby giving rise to a much smaller lumen than is normally the case. Although Krabbe states nothing as to the shifting of the medullary rays, he shows (in two figures) a shifting similar to that found in the

sycamore and maple under the pressure of the bag worm bands.

Küster (7), in an investigation on the union of apposed branches, states that the first effect of the mutual pressure of two such organs, aside from the changed direction of the medullary rays, consists in a flattening of the surfaces apposed, due to growth reduction. An increased growth of the primary bark at the edges takes place. He does not agree with Krabbe as to the activity of the cambium, finding that the growth of the cambium does not remain normal up to the point of union, but that growth stops entirely, because of too great pressure. Before it stops growing, Küster finds that the cambium forms a more or less well developed layer of modified woody tissue, which Krabbe does not mention at all. This modified layer of woody tissue differs from the normal wood in that it is composed of parenchymatous cells, and is to be considered as a parenchymatous tissue. It consists of libriform vessels and parenchymatous cells, which are more or less thickened, pitted and lignified. For the sycamore, Küster states that "it is surprising to see the extraordinary development under the influence of pressure; parenchymatous tissue develops, which starts sharply defined from the normal wood. Outside of this normal wood one finds a thick layer of radially elongated, lignified and very much pitted parenchymatous cells. True wood cells continue to be formed only here and there, and in a cross-section the groups of these wood cells enter into the parenchymatous mass in a wedgelike manner. Finally the formation of even these isolated groups of wood cells stops entirely. . . The pressure is not the physical cause of this growth, but acts only as a stimulus which affects the protoplasm, and the real cause must be sought in the nature of the latter itself." Küster discusses the apparent discrepancy of his own and Krabbe's results, and sees an explanation in the different manner in which the pressure was applied; in

one case with rollers acting for a short period and rapidly applied, while in the case of Küster's unions it started as a slight pressure and, increasing to a maximum, continued for a long period of years until a pressure of 11-17 atmospheres was reached. Küster furthermore calls attention to the change in direction of growth of the cambial cells, which normally form woody cells with their long axes parallel to the axis of the stem, but which under the influence of the pressure change their direction 90 degrees, many of them being curved and bent into "C" and "S" forms. He regards these as originating from bent and displaced cambial cells; their formation being a physical process, and their displacement probably due to the pressure coming only from one side, which gives these cells an opportunity for lateral development.

In the case of the bands of the bag worm, the pressure applied was very similar to that obtained in the investigations of Krabbe, with the exception that the force was applied gradually, and in that manner was more like the pressure obtained by Küster when he caused two branches to join by being pressed together at one side. From the description of the changes which take place in hardwood trees particularly, under the influence of the constriction caused by the bands of the bag worm, it will be noted that these changes are almost identical with those described by Krabbe. In no case is there any evidence of the formation of the parenchymatous tissue spoken of by Küster. Examination of branches of maple, sycamore, red gum, willow, and other hardwoods, showed that in every case, in spite of the enormous pressures that were exerted by the band towards the latter part of the growing season, there was no cessation on the part of the cambium in the formation of typical wood cells, though the last cells formed were very much smaller, just as were those found by Krabbe under his rollers (pl. 25 and 26). I am inclined to agree with Krabbe that the pressure does not in any

way influence the division of the mother cells of the cambium, but that any change which takes place occurs after the wood cells have been formed. The cambial cells divide even under great pressure, though when the pressure reaches a certain point it is probable that the rate of division is considerably reduced. The formation of new cells evidently stops abruptly; in other words, the conditions for the development of new cells from the cambium are such that the latter is able to form these new cells irrespective of the growing pressure up to a certain point, and when this point has been reached growth stops. The cambium appears to be more or less uninfluenced in the character of its cell divisions by pressure exerted upon it, and is able to continue its activity up to a maximum point.

Concerning the discrepancy between the findings of Küster and those of Krabbe and myself, I am inclined to ascribe the formation of the parenchymatous tissue in the branches investigated by Küster to the unequal pressure to which the apposed surfaces were exposed. I have found a tissue which resembles that described by Küster under similar conditions in stems of maple and other trees in the region immediately below twining vines, particularly where the latter caused a constriction in the bark of the trunk around which they were growing.

The change in direction of growth of the cambial cells resulting in a shifting of the axis of the wood cells to an angle of 90 degrees from that usually occupied by them, has already been referred to above.

Summing up the changes which occur in the region of wood under the band, it may be said that with an increase of pressure smaller and smaller cells are formed, because of the inability of the newly formed wood cells to expand to a normal size; the cambium continues forming wood cells of the usual kind but at a decreased rate as the pressure increases. Where the pressure is reduced, at the edges of the band, a shifting of the cambial cells takes place, result-

ing in the turning of the long axis of the wood fibres at an angle of 90 degrees to their usual position.

It has been stated that as soon as the pressure exerted by the band becomes great enough to retard the expansion of newly formed wood cells, an increased growth becomes evident above the band in conifers, and both above and below the band in hard woods. The cambial tissue in the region not acted upon by the pressure at first continues to grow normally, but very soon increases its rate of cell division. Under the changed condition of tension a change of direction of the cambial layer takes place; instead of remaining a sheet parallel to the long axis of the branch, the cambium both above and below the band is curved outward. The wood and bark cells produced, because of this altered position of the cambium, instead of growing in a radial direction, as they do normally, are turned so that their axes gradually approach a direction at an angle of 90 degrees from their normal position. With this changed position in the direction of growth of the wood and bark cells comes an increased development of both, so that after awhile the branch is very much thicker immediately above and below the band than it is at some distance from it. The swellings appear as the lips already referred to.

The tissue composing the two lips is, to all intents and purposes, wood tissue. The tracheids are normal in character, although many of them are somewhat shorter than those formed under normal conditions; there is, in other words, no development of what might be termed callous tissue or anything resembling the tissue known as "wound wood." The development of the lips, in many respects, however, resembles the development of callous tissue after a ring of bark has been removed from a twig. In the latter case, the stimulus, as a result of which an increased development of tissue takes place at the margins of the cut, consists in the interruption of the strains normally active in the growing region of the twig. By cutting away a certain

layer of bark the cambium is free to develop without the restraining pressure exercised by the bark, and as a result grows rapidly in the direction of the least strain. This growth continues until the callous surfaces formed on the upper and lower sides of the wound unite and re-establish the normal pressure conditions. In the case of the constrictions caused by the bands of the bag worm, a similar disturbance is brought about by arresting the development of the cambial layer for a certain distance completely around the twig, and thereby disturbing and probably rendering inactive the normal bark pressures. To all intents and purposes therefore the formation of the lips of the bag worm constrictions may be said to be due to a similar stimulus to that which results in callous formation after a wound, though the formation of the lips is not to be regarded as a callous development, but rather as a new type of healing of a different character.

It is a well-known fact that, where branches are girdled by removing a portion of the bark down to the woody cylinder, the development of callous tissue takes place from the upper or outer edge of the wound. The transfer of carbohydrates and nitrogenous substances takes place in a downward direction from the leaves towards the trunk (Czapek, 1 and 2). Some writers, *e. g.*, Fischer (3), have gone so far as to maintain that the carbohydrates formed in the leaves go downward only in the bark, and that in girdled branches they cannot even be transferred across the wound through the pith or wood parenchyma. Although very little attention has been paid to the problem of nutrition in the healing of the disturbance caused by the bands of the bag worm, it is nevertheless suggestive to note the difference in the manner of healing between the coniferous and hardwood trees. As soon as the pressure exerted by the bands becomes great enough to obstruct the cells of the bark, an evident congestion takes place in the region above the band. In the coniferous trees the food supply is evi-

dently entirely cut off, and as a result practically no growth takes place in the twig on the side below the bands. The portion of the twig above the band continues to grow for a considerable period. The absolute cessation of the passage of starch and other substances from the leaves towards the trunk is well shown by the total absence of starch in the region below the band in the fall of the year, while in the region above the band the wood parenchyma and bark cells are completely filled with starch. In the hardwood trees the pressure of the band is evidently never great enough to entirely obstruct the passage of elaborated materials. No cases were found in the large number examined, with the exception of the locust, where the constriction caused by the band was great enough to prevent the growth of the part below it. In the fall of the year starch is found in the parenchymatous tissue both above and below the band in almost equal quantity. The difference in the behavior of the conifers and the hard woods is a suggestive one, as indicating the greater adaptability of the latter, and their higher grade of physiological organization.

GROWTH ENERGY OF TWIGS AS INDICATED BY THE PRESSURE OF THE BANDS.

It has been stated that in the normal course of events the twigs burst the bands of the bag worm shortly after the beginning of the period of wood formation in the early summer of the second year. Now and then the strength of a band was such, however, that the twig failed to burst it, and as a result the constrictions just described were formed. The bursting of the bands has been explained as due to the force exerted by the twig after it began to grow in diameter. Putting it in another way, the bursting of the band may be said to be due to the growth energy developed by the growing twig. That plants do exert a certain amount of growth energy is a familiar fact. It is well known how the roots of trees will lift the flagstones in the

streets of our cities; the lifting and pushing power of roots and trunks is furthermore frequently noted in the forest, where large boulders are pushed aside or lifted. Another familiar instance of the energy exerted by the growth of plant tissue is found in the roots of most higher plants, which exert a certain amount of energy in pushing aside soil particles. Although this growth energy may sometimes be very large, it frequently is not sufficient to overcome the obstacles to which growing parts are subjected. This is frequently illustrated by roots which grow in the clefts of large boulders — they are frequently unable to burst these, and as a result, are forced into a flattened form. Many climbers exert a sufficient pressure upon the trunks around which they are growing to arrest development. Wires and other bandages frequently bring about girdling of trees very similar to those described for the bag worm.

While it has been realized that the amount of energy exerted by growing tissues may sometimes be very large, very little is as yet known as to how large the amount of energy developed by growing tissue actually is. In the course of the investigation on the constrictions caused by the bag worm bands, it was suggested that these bands might serve to indicate something as to the extent of the growth energy of young twigs. In the largest per cent of the cases the twigs burst the bands; they must therefore exert a radial pressure outward greater than that usually exerted by the band in an opposite direction. A series of experiments was therefore undertaken to determine how great the pressures were which the bands exerted upon the twigs, with the object of using the results as a guide to determine the growth energy of the twig.

Of the investigations hitherto made to determine the extent of the growth energy of plant tissues, there is practically only one which needs consideration. Krabbe (6) undertook some years ago to determine the extent of the growth energy of various trees, by placing bands, consist-

ing of a series of rollers, on the growing branches, and causing these bands to press with varying loads upon the branch, by attaching weights. For the details of Krabbe's method, the reader is referred to his original paper. Krabbe placed different weights on different branches, and after having left them for a season, he made microscopic examinations of the tissues immediately under the band. He attempted by so doing to find what weight, or in other words, what radial pressure, would stop the increase in diameter of the branch. He holds that this weight would be equivalent to the growth energy of the twig.

As a result of his investigations Krabbe concludes that the growth energy of the cambium ring and young wood cells in coniferous trees is at least 10 atmospheres. For hard woods he finds that the growth energy is at least 15 atmospheres. Krabbe was unable to determine the exact value of the expansive force of the limbs and branches with which he experimented. His results simply show that with the greatest pressures exerted by his rollers, viz: 10 atmospheres for conifers and 15 atmospheres for broad-leaved trees, growth still took place under the bands. The figures which Krabbe obtained are to-day in general acceptance as probably representing the approximate minimum growth energy of branches. Friedrich (4) makes the statement that "the increase in diameter of the tree trunk takes place with a development of energy equal to at least 10 atmospheres."

In order to arrive at some conclusion as to the amount of energy required to burst the bands of the bag worm, it was necessary to determine, first of all, the pressure which the bands were capable of exerting radially. The radial pressure exerted by a band placed around a cylinder is determined by the formula

$$P = \frac{S}{r \times w},$$

in which P equals the radial pressure exerted by the band

per square mm. of surface, S equals the strain which the band is capable of exerting tangentially; or, in other words, the strength of the band which resists tearing, r equals the radius of the twig around which the band is fastened, and w equals the width of the band. A number of microscopic examinations were made to determine the variability of thickness in the band, which ought to be included as a factor in the above formula. The variation was found to be so small, however, that for the purpose of the experiment the thickness was left out of consideration. Several hundred twigs from which bag worms were suspended were collected in the spring of the year from shade trees in and near the Missouri Botanical Garden. The tree upon which the bag worm is most commonly found in St. Louis is the soft maple, and the bags found on this tree were made the chief subject of study. Another reason for so doing was that the bands found on the maple twigs were usually of a sufficient size to permit being measured, while those on other trees, and particularly on the conifers, were usually so small that with the apparatus at hand it was impossible to make exact determinations. The method which was used to determine the strength of the bands was as follows: With a sharp knife the bands were cut as near to their union with the bag as possible; the bag with the band was then removed from the twig without difficulty, and a second cut was made in such manner that the band was separated entirely from the bag. A flat sheet was thus obtained, varying from 6 to 12 mm. in length. After the band had been thus removed, a careful measurement was made of its width and of the diameter of the twig from which it was taken. After numerous trials, an apparatus was constructed consisting of a framework, from the top of which a pair of pliers was suspended, with the jaws pointing downward; a similar pair of pliers with the jaws pointing upward was arranged so that a scale pan was attached to its handles. In both cases the pliers were so

arranged that when a pull was exerted on the lower pair the handles of both pliers became more and more firmly compressed, thereby increasing their hold upon the bands placed between the jaws. When ready for the test the bands were carefully straightened, and the ends were placed between the jaws of the two pliers; only enough of the band being caught by the pliers to give a firm hold. Very fine shot was then gradually put into the scale pan attached to the lower pair of pliers until the band broke; the weight of the shot, plus that of the pan and lower pair of pliers, constituted the breaking weight of the bands.

It was at first thought that the weakest point in the bands would be where the bands were fastened to the bag; in order to determine whether this was the case, a number of tests were made by attaching weights to the bags themselves, and increasing the weights until something gave way. In every one of the preliminary tests the break in the band occurred at some point away from the bag attachment. In other words, it appeared that the weakest part of the band was not at or near the bag attachment. It was therefore considered to be perfectly fair to cut away the bag and to enclose the ends of the bands between the jaws of the pliers; the results obtained by breaking hundreds of the bands bore out these preliminary conclusions. It was found that in almost all cases the bands broke at some point between the jaws of the two pairs of pliers and not immediately at the edge of the jaws. It was furthermore noted that under most conditions where the bags were attached to twigs on the growing tree the break in the band occurred in a similar manner to that found when weights were attached to the bags themselves. An examination of a large number of bands made during June showed that with the increase in diameter of the twigs which brought about the bursting of the bands on the trees, the bursting of the band took place at a point away from the bag insertion.

The results obtained were calculated according to the formula given above; and, following Krabbe's method, the final figures were calculated to show the pressures in grams per square millimeter of bark surface, which were then reduced to atmospheres of pressure. For this purpose 10 grams were used as equivalent to 1 atmosphere of pressure per square millimeter. In the case of the maple some 400 bands were tested. It is proposed to test a great many more bands in the future in order to have a larger number of figures to work with.

Before drawing any conclusions as to the results of the strength tests, it should be stated that the use of the bands as an indication of the amount of growth energy exerted by the twig must be taken with some caution. No claim is made that the results to be discussed are in any way absolute; the bands are an extremely variable quantity; they differ in width and thickness, and the error in measurement is consequently to be considered. It was furthermore suggested that there might be a very decided difference in the strength of the bands, depending upon whether they were wet or dry, and likewise upon their age. The former point was considered of great importance, and accordingly a large number of bands were broken after they had been soaked in water for five days. It was thought possible that as a result of wetting during rains in the early summer, the bands might be considerably weakened, and that it would be at such a time that they were burst by the twigs. The results obtained from the tests with soaked bands in no way differed, however, from those obtained with dry bands, and it is accordingly the belief that the soaking practically does not weaken the bands at all, or at least very little. Concerning the effect of age, most of the bands were taken and tested during May and June, *i. e.*, after they had been exposed to the weathering influences during the fall and winter. It is therefore be-

lieved that if the weather exposure weakens them, they were tested at the time when they were weakest.

The first analysis of the measurements made deals with the size of the bands and their relation to the size of the twigs to which they were attached. It has already been stated that attempts were made to cause the insects to weave bands around large twigs, but in every case the insect refused to do so. On Table I the bands taken from

RELATION OF DIAMETER OF MAPLE TWIGS TO WIDTH OF BAND.

Width of Band. mm.	Diam. of Twig. mm.	1.5	2	2.5	3	3.5	4	4.5	5	5.5	Total Bands of one width.
1			3	2	1	6	2				14
1.5				2	13	6	2				23
2		1	11	22	46	16	12	3	2	1	114
2.5			4	16	28	12	5				65
3		1	11	22	52	16	13	5	1	1	122
3.5		1	4	4	11	6	3	1			30
4			4	5	10	1	5	1	1	1	28
4.5				1		2					3
5				2	4		1		1		8
5.5									1		1
6					1						1
6.5											0
7					2						2
7.5			1								1
8					1						1
Total bands per twig		3	38	76	169	65	43	10	6	3	413

TABLE I.

maple twigs are arranged according to their width and according to the diameter of the twigs. It will be noted that the largest number of bands occurred on twigs 3 mm. in diameter, and that there is a regular falling off towards both sides; in other words, the insect seems to select twigs having a diameter of about 3 mm.

Concerning the width of the bands, there is more variation. Of the 413 bands, 122 were 3 mm. in width, 65 were 2.5 mm. and 114 were 2 mm., in decreasing numbers of smaller and greater widths. The largest number occurring on any particular diameter of twig were 3 mm. in width. Preference for the twigs 3 mm. in diameter is furthermore shown on Diagram 2, a, representing the relation of strength, using the twigs of different widths as the variable, and Diagram 2, b, where the bands of different widths are used as the variable. The final results obtained with bands taken from maple twigs are plotted in Diagram 1; the figures at the bottom of the table indicate the number of atmospheres pressure exerted by any band upon the particular twig which it subtended. The figures at the left of the table represent the numbers of individual bands exerting any particular number of atmospheres pressure. There were, as may be seen from this, four bands which exerted a pressure of 10 atmospheres and 16 which exerted a pressure of 19 atmospheres each, etc. While the number of bands which were broken was a rather small one for the purpose of any definite statistical study, enough were tested, nevertheless, to show a number of interesting facts. The radial pressure exerted by the bands varied from 4 atmospheres to 162 atmospheres in the case of the maple. The greatest number of the bands varied between 14 and 44 atmospheres. The strength which some bands showed was surprising. On Table II a number of instances of extreme strength are shown for maple and other trees. The deductions which may be made in a tentative way from the results shown in Diagram 1 are as follows: A great variation in the pressures exerted by the bands of the bag worm on the twigs of maple trees exists. Some of these pressures are very great, and it is probable that bands like those which showed pressures of 102 to 162 atmospheres are the ones which are responsible for the

constrictions described above. Remembering that most of the bands which occur on maple twigs are burst by the twig every year (only 1.5–2 per cent are not burst), it seems probable that the larger number of bands represented in this table would have been burst during the growing period. As many of these show that these bands exert radial pressures running up to 40 atmospheres and more, it seems

EXCEPTIONALLY STRONG BANDS.

Tree on which bags occurred.	Width of band. mm.	Diam. of twig. mm.	Total Breaking weight. grams.	Atmospheric pressure.
White Pine	1.5	1.5	935	83.1
	3	2	2275	75.8
	3	2	2472	82.4
	1	2	650	65.0
	2	1.5	1090	72.7
Maple	3	3	3202	71.1
	3	3	4324	96.8
	1	2	668	133.6
	2.5	3	3727	100.7
	3	2	3632	121.1
	.5	4	1620	162.0
Sycamore	3	2.5	1778	177.9
Willow	1.5	1.5	1217	108.1
	2.5	2.	3272	130.8
	3.5	3	4737	90.2
	2	1.5	1632	108.8
	2.5	1	1775	158.0
	2	2	2130	106.5
	1.5	1	900	120.0
	2	2	2350	117.0
	4	2	3675	91.9

TABLE II.

likely that the pressure which the twigs are capable of exerting radially must be at least equivalent to these pressures in order to burst the bands. It will be remembered that the figures which Krabbe obtained, showing that the pressure exerted by growing twigs of hard woods was 15 atmospheres or thereabouts, in no way indicated what the upper limit might be. Judging from the structure of the wood which he shows, cell division was still taking place

with considerable activity under the bands weighted so as to exert a pressure of 15 atmospheres, and Krabbe states distinctly that the growth energy must therefore be equivalent to *at least* 15 atmospheres. As a result of the few tests herein described, I am inclined to the belief that the pressures are probably very much higher than 15 atmospheres. Owing to the variability of the bands it does not seem practicable, particularly with the small number of bands tested and in the absence of determinations as to their thickness, to place any absolute value upon the growth energy as determined by the bands. That the growth energy exceeds 15 atmospheres seems very probable, and I am inclined to the belief that it may reach the extent of 30 to 40 atmospheres, and possibly more. As a matter of statistical interest, Diagram 2, a and b, is added. The upper diagram (a) shows the relation between the strength of bands of different width, and the lower one (b) the relation between the strength of bands found on twigs of different diameters. Both of these tables show that the bands of greatest strength are those that are attached to twigs of 3 mm. in diameter.

BIBLIOGRAPHY.

1. Czapek, Fr. Über die Leitungswege der organischen Baustoffe im Pflanzenkörper. (Sitzungsber. d. Kais. Akad. d. Wiss. zu Wien, Math. Naturw. Cl. **106** : 117. 1897).

2. Czapek, Fr. Zur Physiologie des Leptoms der Angiospermen. (Ber. d. D. Bot. Ges. **15** : 124. 1897).

3. Fischer, A. Beiträge zur Physiologie der Holzgewächse. (Pringsh. Jahrb. f. Wiss. Bot. **22** : 73. 1891).

4. Friedrich, Josef. Über den Einfluss der Witterung auf den Baumzuwachs. (Mitth. aus d. Forst. Versuchswesen Oesterreichs. **22** : 1897. — Ref., Bot. Zg. **55** : 368. 1897).

5. Krabbe, G. Über die Beziehungen der Rindenspan-

nung zur Bildung der Jahrringe und zur Ablenkung der Markstrahlen. (Sitzungsber. der Kgl. Preuss. Akad. d. Wiss. **51**: 1093. 1882).

6. Krabbe, G. Über das Wachstum des Verdickungsringes und der jungen Holzzellen in seiner Abhängigkeit von Druckwirkungen. (Sitzungsber. d. K. Preuss. Akad. d. Wiss. **53**: 57, 69. 1884.— Also Separat aus Abh. d. K. Preuss. Akad. d. Wiss. 1884).

7. Küster, E. Über Stammverwachsungen. (Prings. Jahrb. f. Wiss. Bot. **33**: 487. 1899).

8. Sachs, J. Lehrbuch der Botanik. 409. 1868.

9. de Vries, H. De l'influence de la pression du liber sur la structure des couches ligneuses annuelles. (Extrait des Archives Néerlandaises. 1876).

EXPLANATION OF PLATES.

Plate 20. — Constrictions caused by the bands of the common bag worm (*Thyridopteryx ephemeraeformis* Haworth) on branches of arbor vitae (*Thuja occidentalis*). Natural size.

The two upper figures are living branches. The lowest one shows a branch killed by the band of the bag worm.

Plate 21. — The bag worm on living one-year-old branches, as it appears a month after the attachment of the bags, usually about the end of September. The upper figure shows it on a sycamore branch, the lower on a branch of the ash-leaved maple. Natural size.

Plate 22. — Constrictions caused by the bag worm on maple twigs of various ages. 1. Twig two years old showing early stage of constriction. 2. Twig 2 years old, showing beginning of union of two lips. 3. Twig 3 years old with healing almost complete. 4. Branch ten years old, healing complete, and top of bag partially overgrown by the wood. Natural size.

Plate 23. — Constrictions caused by the bag worm in various hardwood trees. 1. On willow. 2. On locust. 3. On sycamore. 4. On red gum. 5. On sassafras. 6. On poplar. 7. On white oak. 8. On apple. $\times \frac{1}{2}$.

Plate 24. — Constrictions caused by the bag worm on various coniferous trees. 1. On *Pinus virginiana*. 2. On *Thuja occidentalis*. 3. On bald cypress. 4. On larch. 5. On Deodar cedar. 6. On hemlock. 7, 8. On Deodar cedar. $\times \frac{1}{2}$.

Plate 25. — Cross sections showing structure of normal wood, and wood from the bag worm constrictions. 1. Normal wood of the soft maple. 2. Wood of the soft maple taken from a point immediately under

the band of the bag worm where growth had stopped entirely. 3. Normal wood of the red gum. 4. Wood of the red gum taken from a point immediately under the band of the bag worm where growth had stopped entirely. $\times$ 400.

Plate 26. — Photomicrographs showing the cross sections of wood taken at points immediately below the bands of the bagworm. The bands were situated at the top of both figures. Upper figure, from a maple constriction. Lower figure, from a red gum constriction. $\times$ 50.

DIAGRAMS.

Diagram 1. — Showing the number of atmospheres pressure exerted by the bands of the bag worm, and the frequency with which the various pressures are exerted among 413 bands. The abscissae show the number of atmospheres pressure; the ordinates indicate the number of individual bands exerting any given pressure.

Diagram 2. — a. The relation between the varying widths of bands and the strength of the bands, expressed in terms of number of atmospherespresssure. The abscissae represent the number of atmospheres; the ordinates the number of individuals. — b. The relation between the varying diameters of twigs and the strength of the bands found encircling them, expressed in terms of number of atmospheres pressure. The abscissae represent the number of atmospheres; the ordinates, the number of individuals.

TEXT FIGURES.

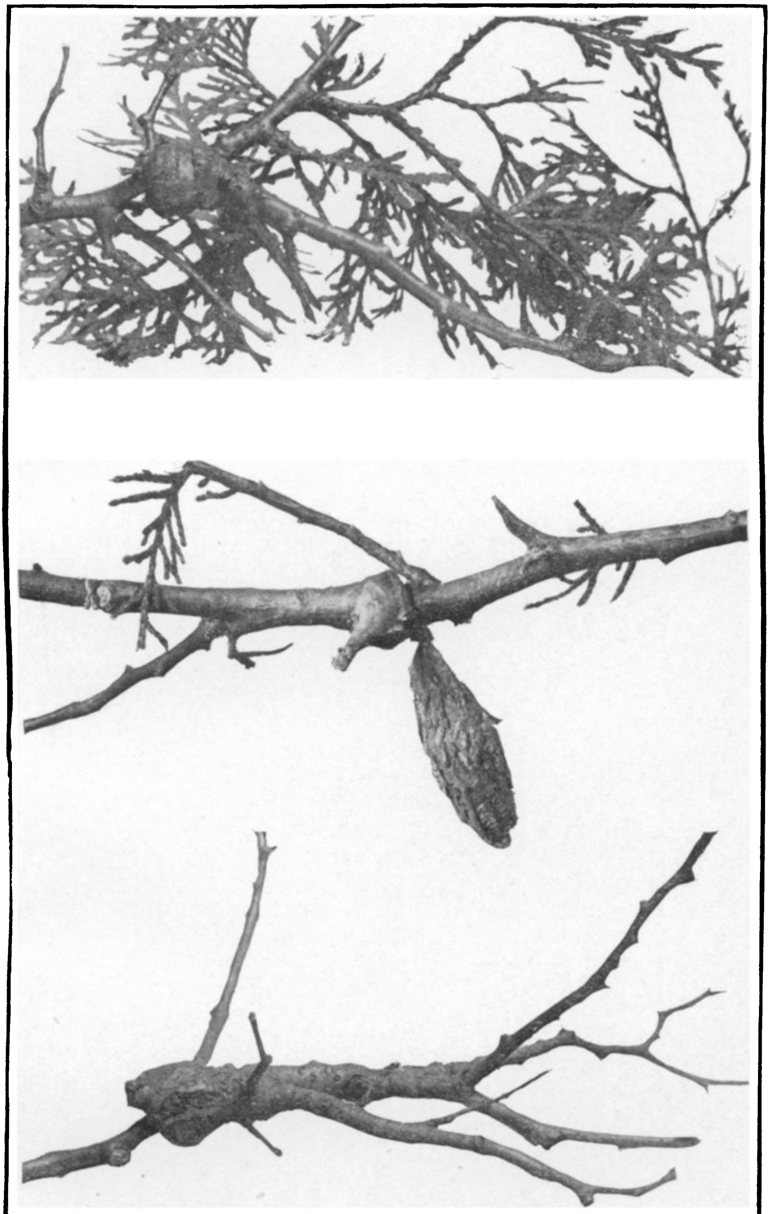
Figure 1. — Longitudinal section through an old swelling of the arbor vitae (*Thuja occidentalis*), showing how the upper or outer portion grew in diameter, while the part below the band stopped growing entirely. (P. 159).

Figures 2-4. — Longitudinal sections through constrictions of the soft maple, caused by the band of the bag worm. The figures show successive stages of healing. Figures 2 and 3 show the top of the bag at the left of the constriction. (P. 160, 161).

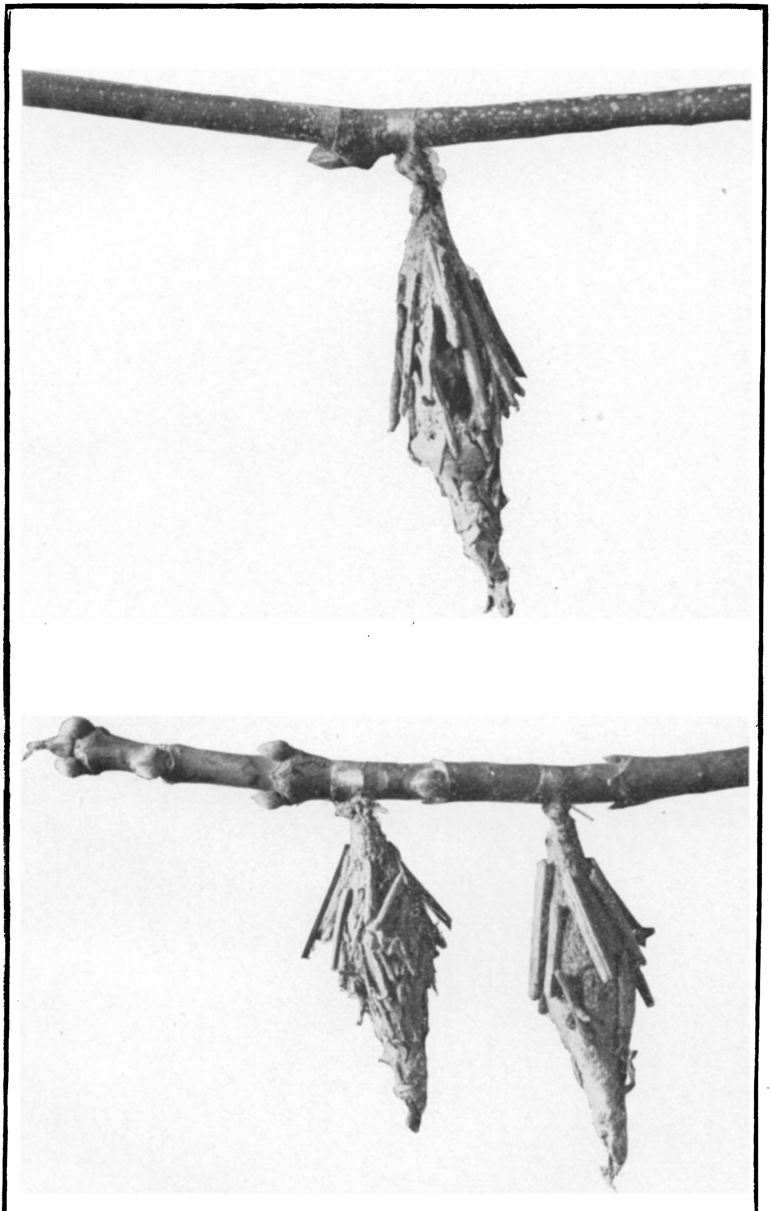
TEXT TABLES.

Table I.—Showing the relation of the diameter of maple twigs to the width of the bands of the bag worm which were found upon them. (P. 176).

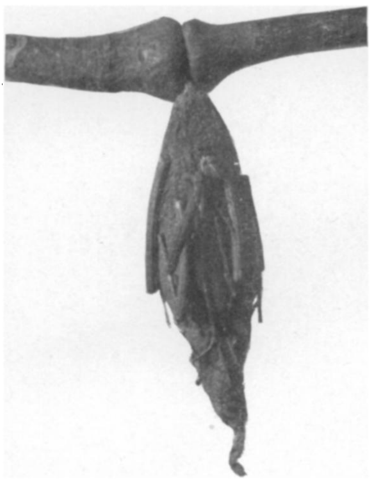
Table II. — Showing a number of exceptionally strong bands, their dimensions and the trees they were found on. (P. 178).



CONSTRICTIONS OF ARBOR VITAE.



BAG WORMS—FIRST YEAR.



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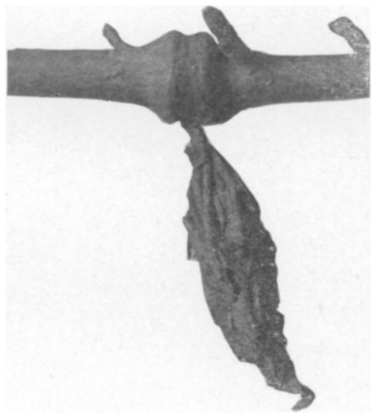

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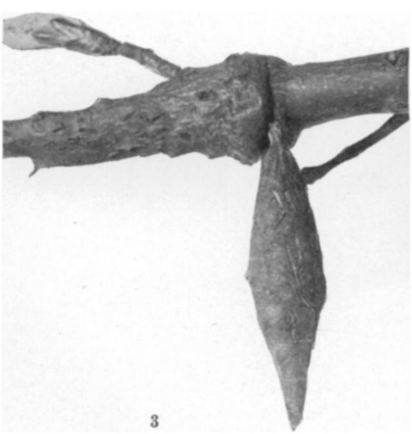

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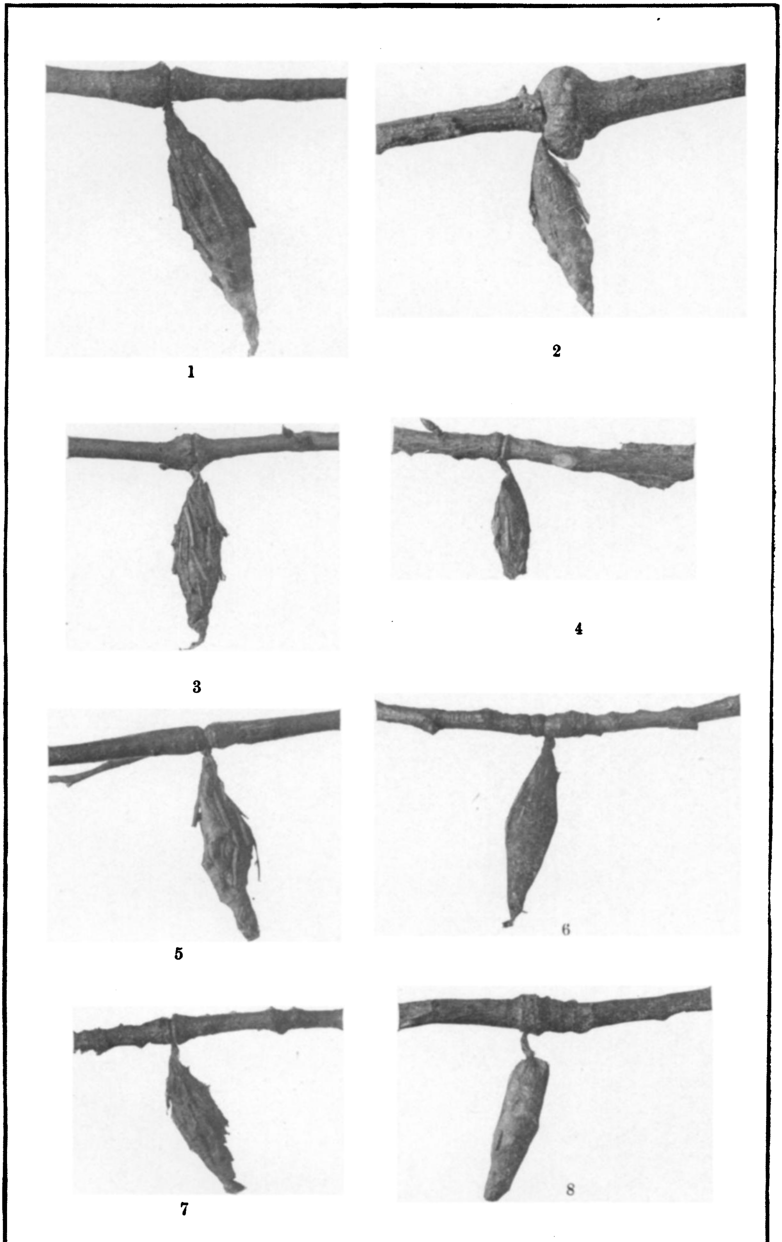
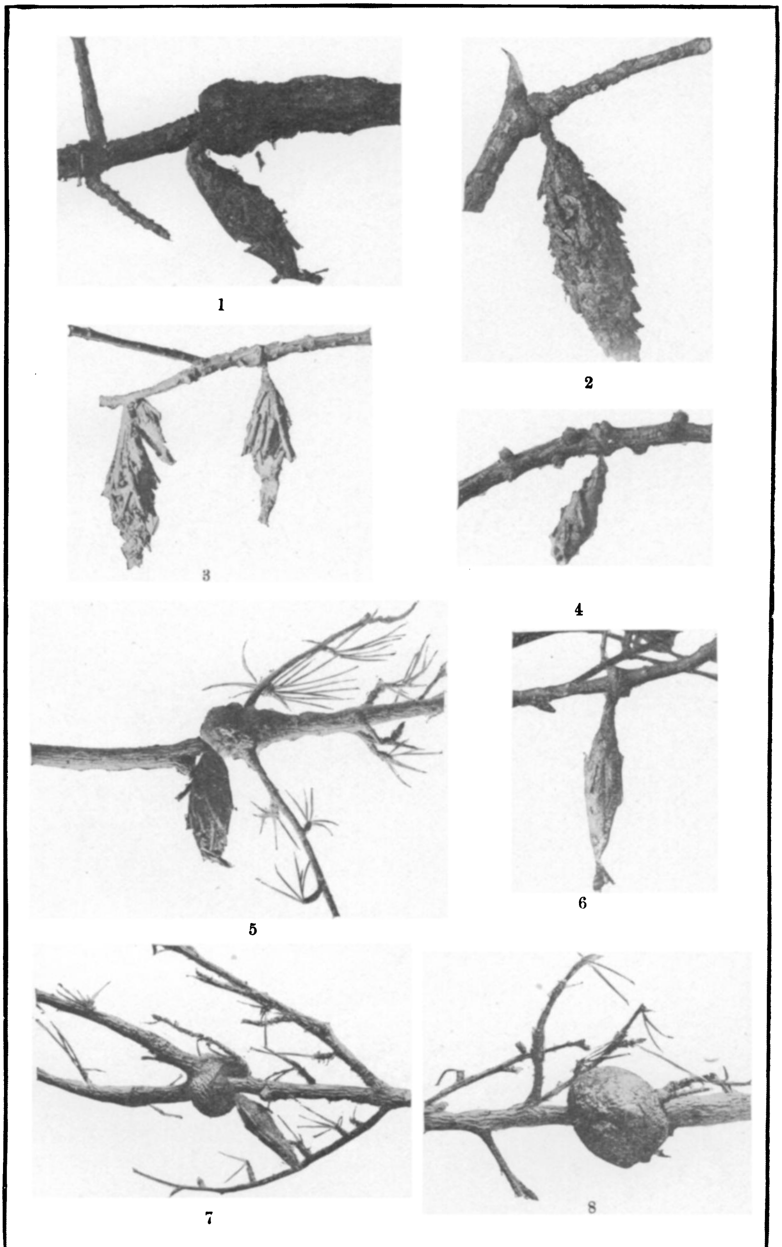
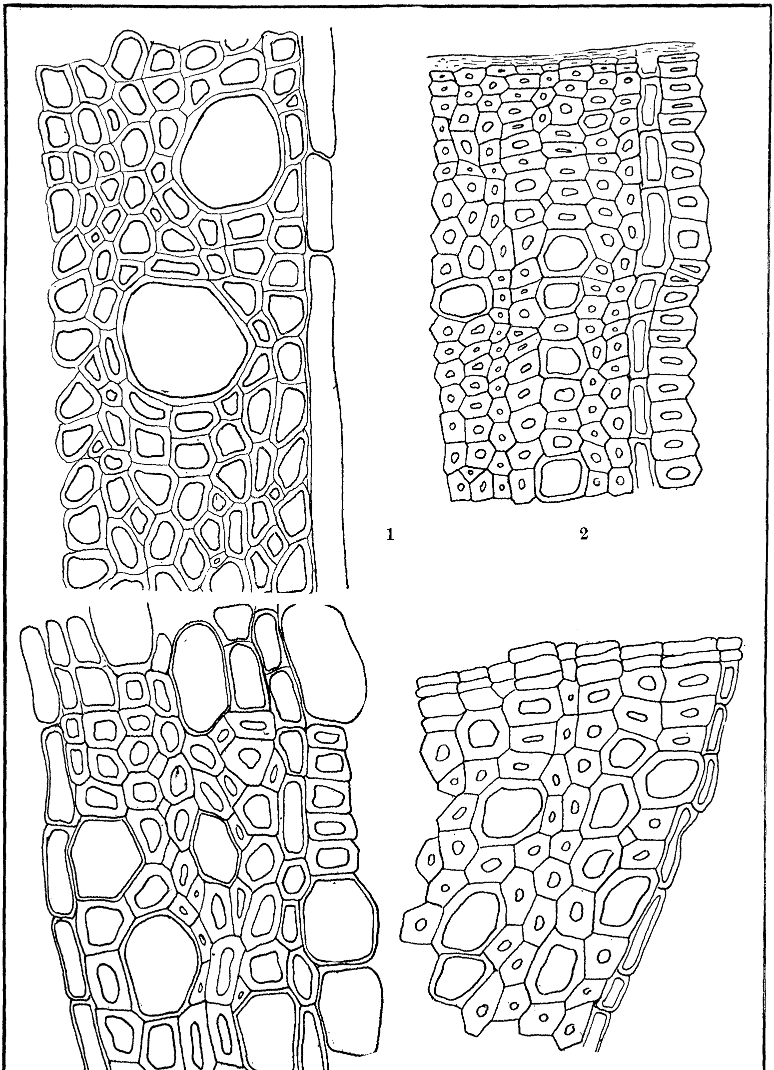
CONSTRICTIONS OF SOFT MAPLE.



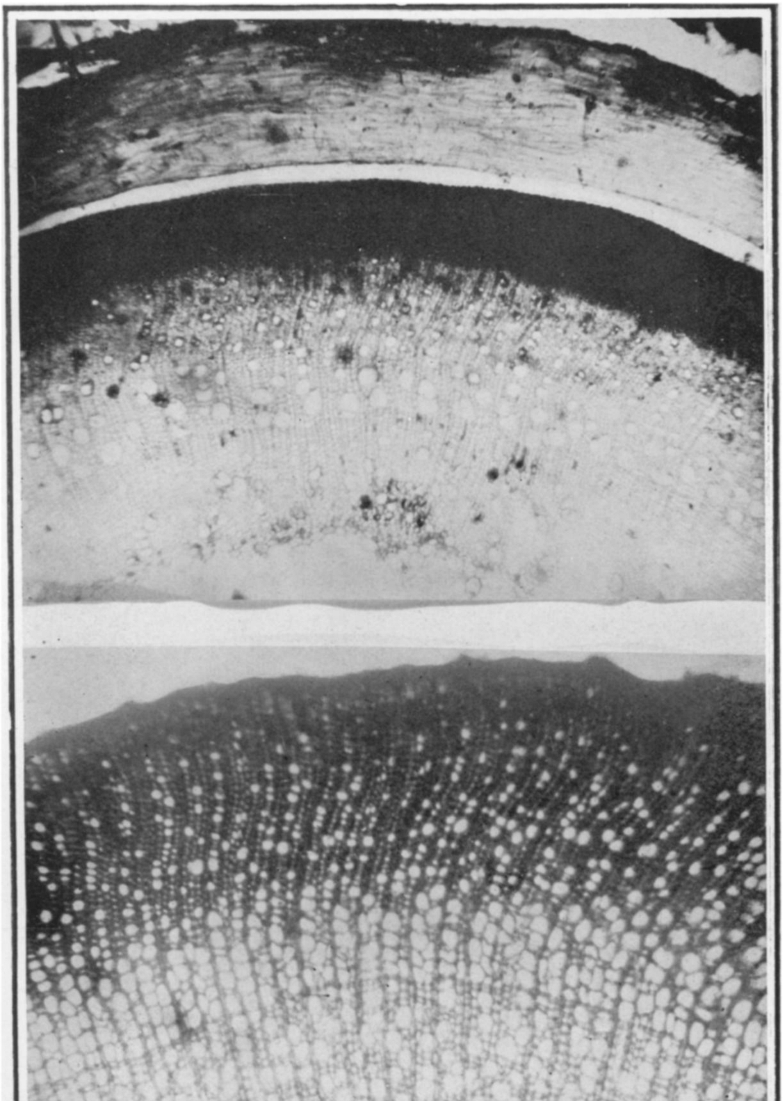
CONSTRICTIONS OF HARDWOODS.



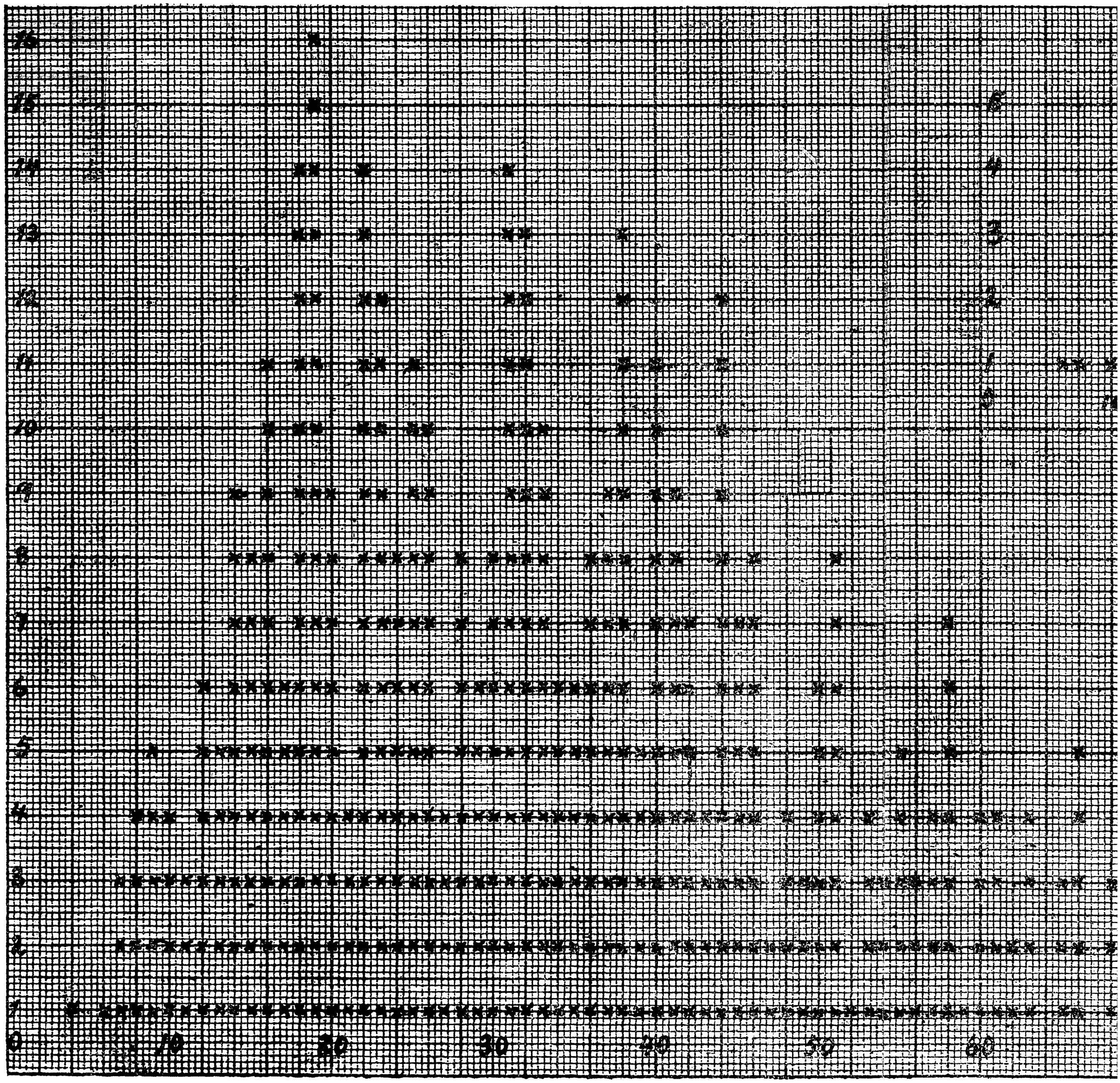
CONSTRICTIONS OF CONIFERS.



NORMAL AND CONSTRICTED WOOD.



WOOD BELOW BANDS.



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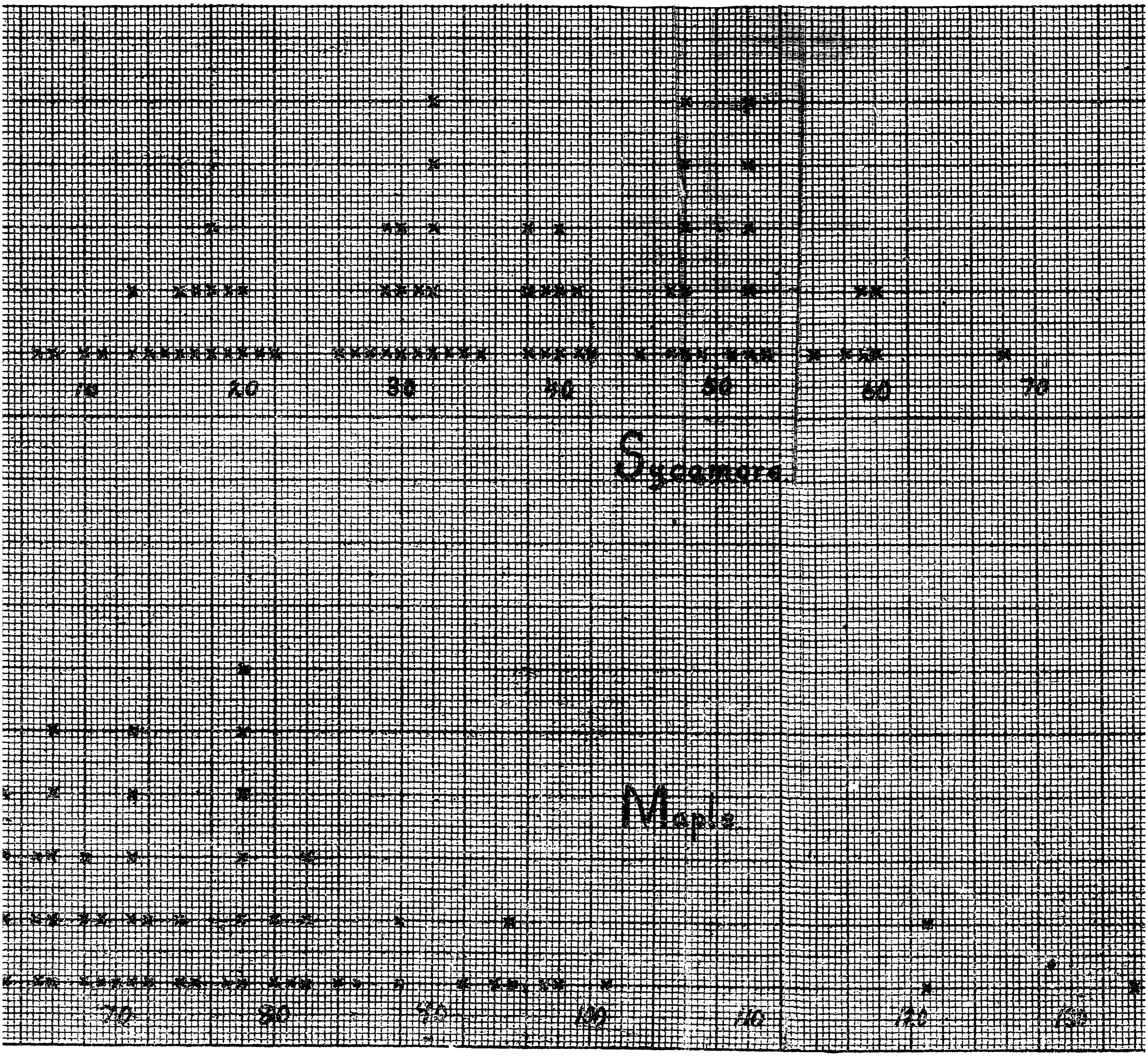
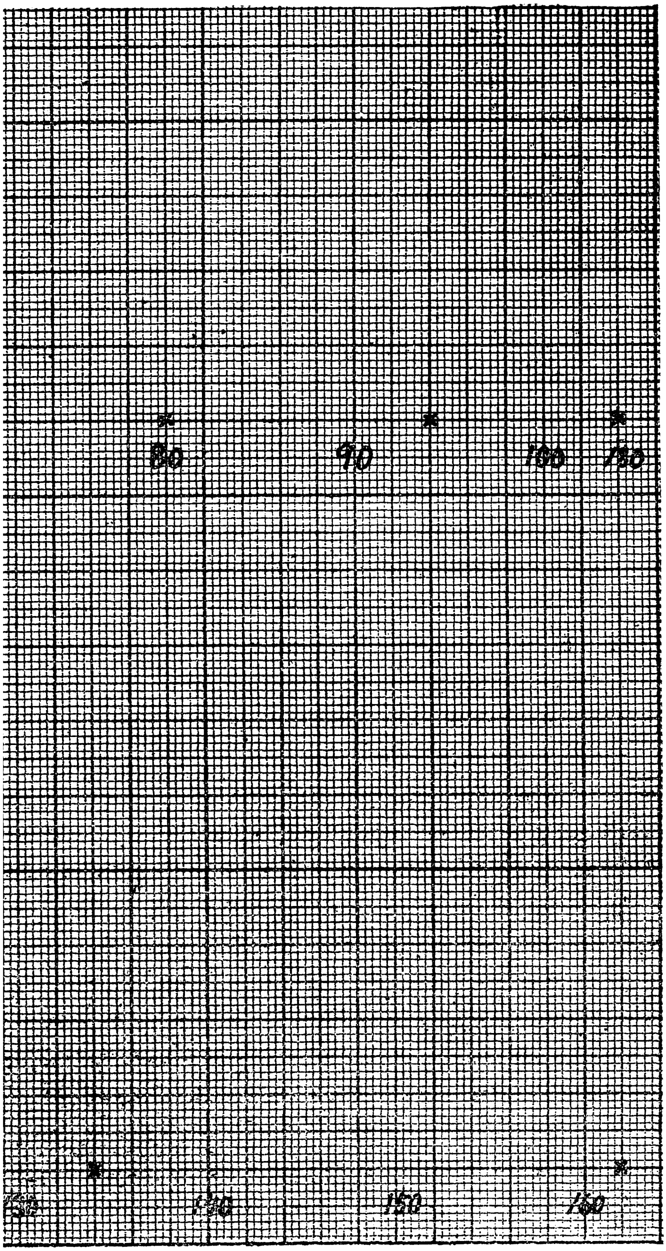
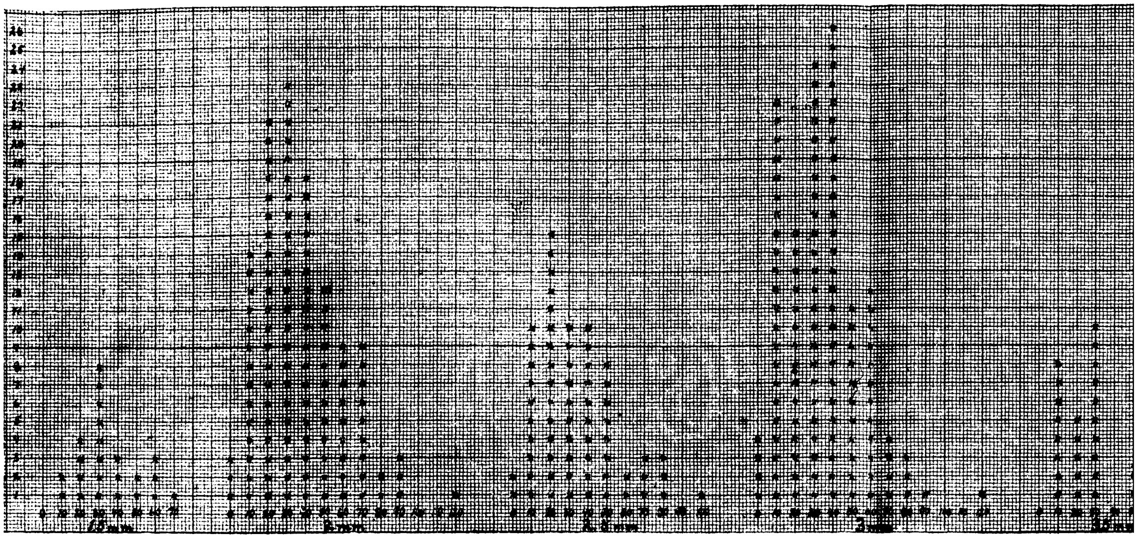


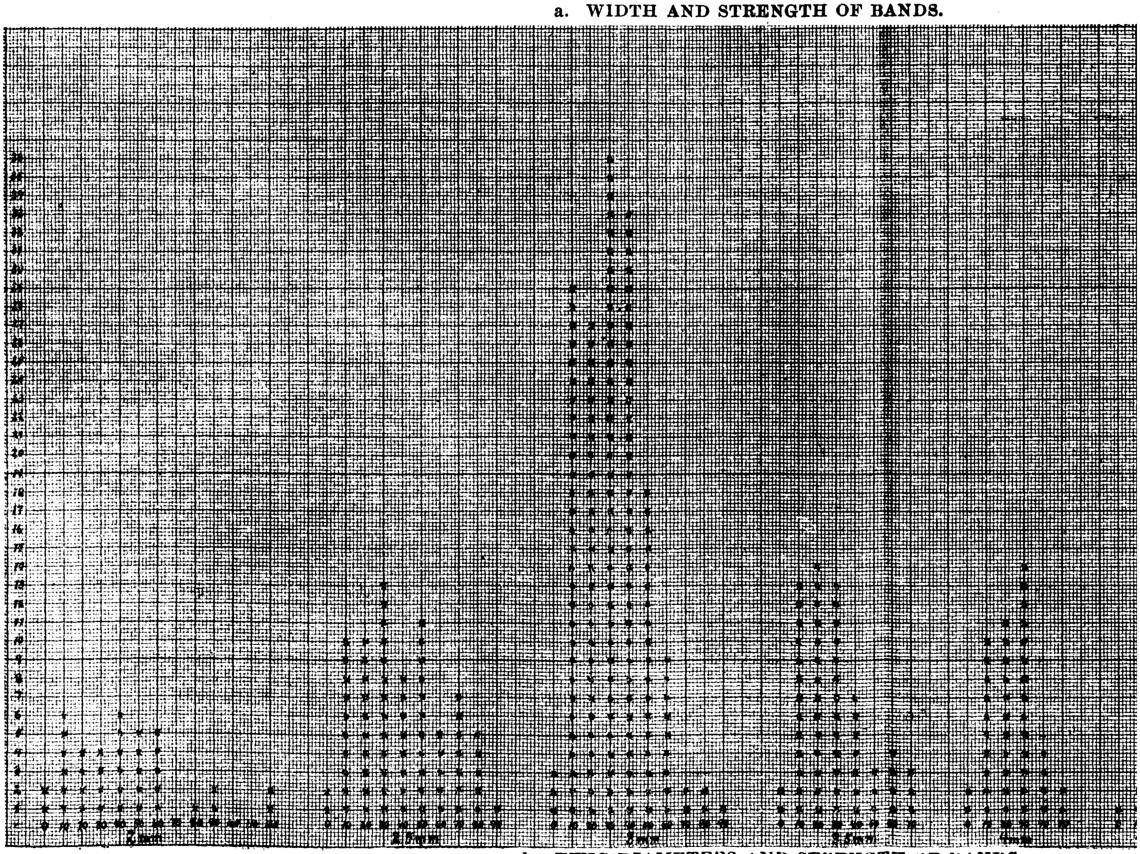
PRESSURE EXERTED BY BANDS.

DIAGRAM 1.

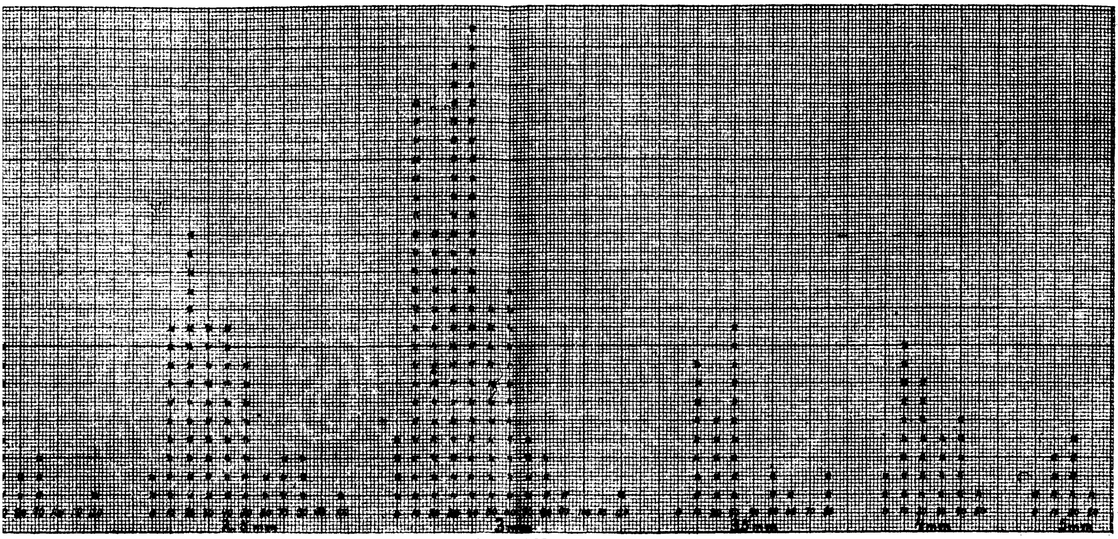




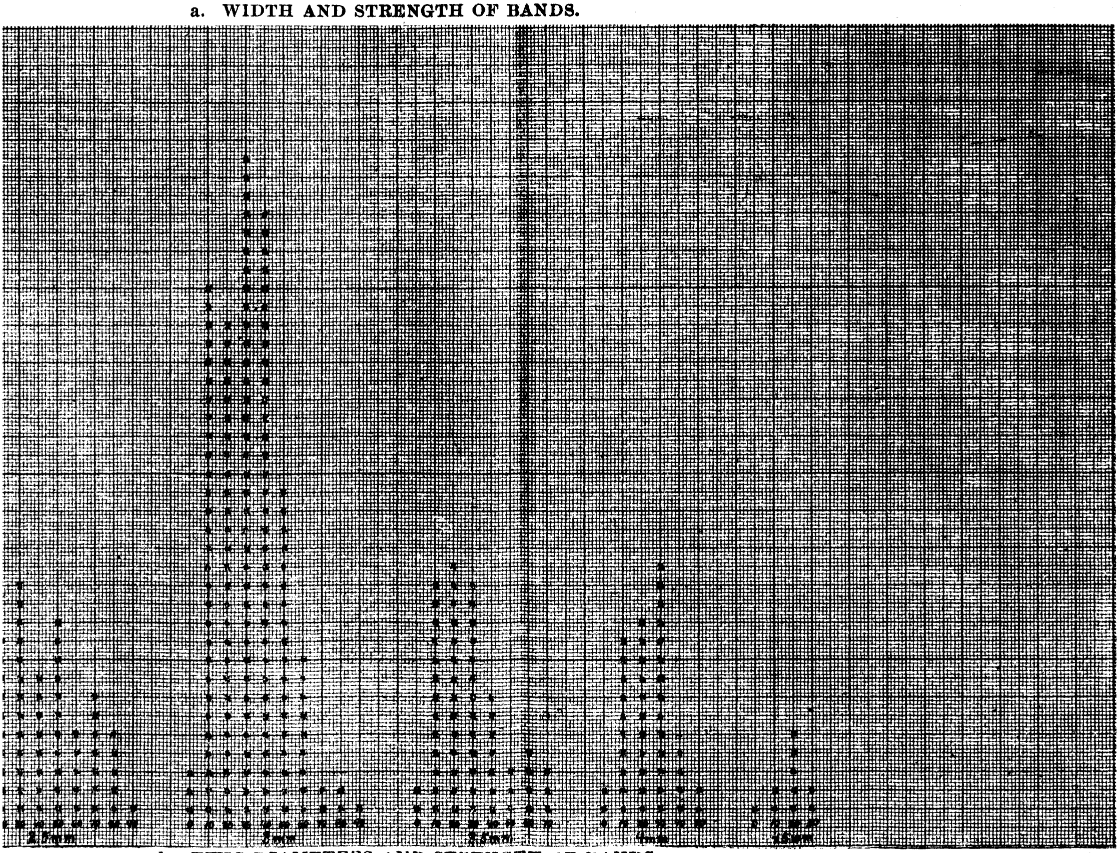
a. WIDTH AND STRENGTH OF BANDS.



b. TWIG DIAMETERS AND STRENGTH OF BANDS.



a. WIDTH AND STRENGTH OF BANDS.



b. TWIG DIAMETERS AND STRENGTH OF BANDS.